

SUPERNUMERARY CHROMOSOMES IN *ERIOPHYLLUM LANATUM* AND
E. CONFERTIFLORUM VAR. *CONFERTIFLORUM* (ASTERACEAE)

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ABSTRACT

Chromosomes in excess of the basic complement have been known for 100 years. Nevertheless, in most species the role of supernumerary or B chromosomes remains unknown or speculative. Here, I describe the frequency, distribution, and transmission to progeny of supernumerary chromosomes in two widely distributed western North American polyploid complexes. Meiotic analyses of microsporocytes found one to four supernumerary chromosomes in 14% of the 293 populations examined in *Eriophyllum lanatum*, and one, two, or six supernumeraries in 15% of the 133 populations examined in *E. confertiflorum* var. *confertiflorum*. Most supernumerary chromosomes were in the size range of A chromosomes, indistinguishable from As, and did not pair with them. Artificial hybridizations showed that the supernumerary chromosomes were transmitted by either parent. Populations with supernumerary chromosomes were nonrandomly distributed in both species. Intervarietal or interspecific hybridization may be responsible for some of their nonrandom distribution in *E. lanatum*. Supernumerary chromosomes may be involved in the dysploid chromosome numbers in *Eriophyllum*.

Key Words: Asteraceae, dysploidy, *Eriophyllum*, polyploid complex, supernumerary chromosome distribution, supernumerary chromosome frequency, and supernumerary chromosome transmission.

Wilson (1925, pp. 872–878) referred to chromosomes in excess of the basic complement as “supernumerary.” He distinguished between those that arose by nondisjunction and others derived by fragmentation. Chromosomes in excess of the basic “A” complement that do not pair with A chromosomes and have certain other characteristics are more often referred to as “B” rather than “supernumerary” or “accessory” chromosomes. Chromosomes in excess of the basic complement are generally smaller than the A chromosomes, do not pair with them but can pair with each other, and often are more heterochromatic than the A chromosomes (Soltis 1983).

The number of supernumerary chromosomes may vary in the same plant, e.g., *Poa trivialis* L. (Bosemark 1957) or in different plants of the same population, e.g., *Xanthisma texanum* DC (Semple 1974). In *Clarkia unguiculata* Lindley, the frequency of individuals with supernumeraries varied from 0 to 79% in different populations, and, in one population, varied significantly in different years (Mooring 1960).

In some species, supernumerary chromosomes can be transmitted or increased in number, as in several grass species (e.g., *Festuca arundinacea* Schreber [Bosemark 1957], or in *Clarkia unguiculata* [Mooring 1960]). Rosato et al. (1996) reported that the transmission of B chromosomes in wild races of maize was under genetic control.

Whether these extra chromosomes are genetically inert, parasitic, or of some adaptive value is unclear, and may well depend on the species

studied. Adaptive effects of supernumerary chromosomes are known or surmised; for example, Bosemark’s (1956) study of *Festuca pratensis* Hudson found a correlation between the clay content of the soil in most Swedish provinces and the frequency of accessory chromosomes. The number of species reported to carry these extra chromosomes has increased sharply in the last 50 yr; about 2000 are known in many taxonomic groups of animals and flowering plants (see Palestis et al. 2004).

Background of Present Study

Eriophyllum lanatum (Pursh) Forbes and *E. confertiflorum* (DC.) A. Gray are polyploid complexes (Mooring 1975, 1994, 2001). *Eriophyllum lanatum* is a short-lived, woody-based, herbaceous perennial; *E. confertiflorum* var. *confertiflorum* is a subshrub. Both are highly self-incompatible. *Eriophyllum lanatum* is widely distributed in western North America from 5 to 3500 m; *E. confertiflorum* var. *confertiflorum* occurs from central California to adjacent Baja California from 5 to 3000 m.

Artificial hybridizations show barriers to interbreeding in both species complexes. Those in *E. confertiflorum* var. *confertiflorum* are weaker; consequently, the races are harder to delimit (Mooring 1994). Interbreeding barriers in *E. lanatum* are stronger; the 10 “varieties” of *E. lanatum* are geographic subspecies (Mooring 2001). Artificial hybrids have been obtained between *E. confertiflorum* var. *confertiflorum*

and all varieties of *E. lanatum* (Mooring 2001 and unpublished). Natural hybrids between *E. lanatum* and *E. confertiflorum* var. *confertiflorum* are frequently encountered (Constance 1937; Mooring 1994). *Eriophyllum latilobum* Rydb. may be a product of such interspecific hybridization (Constance 1937; Munz 1959).

My report is an offshoot of long-term bio-systematic studies of *Eriophyllum lanatum* (Mooring 1975, 2001) and *E. confertiflorum* (Mooring 1994). Those studies focused on the distribution of cytotypes and on barriers to interbreeding at the diploid level. The supernumerary chromosomes in both species presented interesting problems, but time and space requirements prevented further study.

The supernumerary chromosomes of *Eriophyllum lanatum* and of *E. confertiflorum* var. *confertiflorum* are in the size range of the smaller members of the basic complement. They do not seem to differ from the A chromosomes in appearance or behavior. With one apparent exception, they do not pair with an A chromosome. Thus, they resemble the supernumerary chromosomes of *Clarkia unguiculata* (Lewis 1951; Mooring 1960). Lewis (1951) believed that these extra chromosomes originated as trisomics.

The distribution and frequency of supernumerary chromosomes, especially in *E. lanatum*, suggest an adaptive role or meiotic drive, or both. Artificial hybridizations have shown that supernumeraries could be transmitted, but have not documented the frequency of transmittal (Mooring 2001).

Thus, in 2000, I began reciprocal crosses in *E. lanatum*: $8 \text{ II} \times 8 \text{ II} + \text{one supernumerary chromosome}$ and $8 \text{ II} \times 8 \text{ II} + \text{two supernumerary chromosomes}$. I present my findings about both species in one report because the species are closely related and the results of each study are similar. The purpose of this paper is to report the frequency, geographic distribution, and transmission of supernumerary chromosomes in *E. lanatum*, *E. confertiflorum* var. *confertiflorum*, and their putative hybrid derivatives.

MATERIALS AND METHODS

Species

Most of the plants used in this study were grown from fruits collected from natural populations; a few were transplants from these populations. The location of the *Eriophyllum lanatum* and *E. confertiflorum* var. *confertiflorum* natural populations are given in Mooring (2001) and Mooring (1994), respectively.

Treatments

Fruits were germinated in vermiculite or in vermiculite-soil mixtures. Seedlings were potted

in "UC Mix" soil in an unheated Santa Clara University greenhouse.

Meiotic Analyses

Young capitula were fixed in 1:3 acetic ethanol or, rarely, in 1:3:6 acetic-chloroform-ethanol. Quickly putting collections in the refrigerator or an ice-filled cooler usually improved fixation (Anderson 1996). Beek's (1955) technique often provided clearer preparations. Most meiotic analyses were of diakinesis or first metaphase stages of microsporocytes squashed in acetocarmine and examined with a phase contrast microscope. Squashing anthers in 1% aceto-orcein instead of aceto-carmine often resulted in more darkly stained chromosomes. Voucher specimens have been deposited in the Santa Clara University Herbarium (SACL).

In this study, chromosomes in excess of the basic complement of *Eriophyllum lanatum* and *E. confertiflorum* var. *confertiflorum* are called supernumerary chromosomes rather than B chromosomes or accessory chromosomes. Because the *Eriophyllum* supernumerary chromosomes were morphologically indistinguishable from the chromosome of the basic complement ("A" chromosomes) at meiosis, I did not distinguish between A and supernumerary chromosomes in reporting meiotic configurations. The letter "I" is used to refer to an unpaired chromosome. Fragment chromosomes were also present, and are called fragment chromosomes.

Artificial Hybridizations

All hybridizations were performed in a pollinator-free greenhouse. The plants were separated by at least 30 cm. Capitula were rubbed together over 2–8 d.

Pollen Fertility Estimates

Fresh pollen grains were stained overnight in cotton blue-lactophenol. Estimates rest on 300 grains per sample. Each plant was sampled on two different days.

RESULTS

Viability of Plants with Supernumerary Chromosomes

Plants with supernumerary chromosomes could be detected only by meiotic analysis. Pollen fertility varied widely in plants with and without extra chromosomes, but no significant differences were found.

Number of Supernumerary Chromosomes per Plant

I found one to four supernumerary chromosomes in *Eriophyllum lanatum*; and one, two, or

six supernumerary chromosomes in *E. confertiflorum* var. *confertiflorum*; and two in *E. latilobum*, a putative *E. lanatum* × *E. confertiflorum* var. *confertiflorum* hybrid (Tables 1 and 2).

Meiotic Configurations

In *E. lanatum*, diploids not derived from artificial hybridizations, one plant formed 8 II + 1 I in most microsporocytes, and 7 II + 1 III in others. The 7 II + 1 III configuration, if due to a chiasma rather than sticky chromosomes, suggests that in this instance a supernumerary can pair with A chromosomes. In all other such diploids, those with one supernumerary formed 8 II + 1 I. In a few cells scored as having 8 II + 1 I, the I divided at first metaphase, and 9 + 9 separations occurred in first anaphase cells. Conspicuously lagging chromosomes in first or second division were rare. Most plants with two supernumeraries formed 8 II + 2 I or 9 II. The single plant with 19 chromosomes formed 9 II + 1 I. One of the two plants with 20 chromosomes formed 10 II exclusively, the other variously 10 II, 9 II + 2 I, and, in a few cells, 8 II + 1 IV (Table 1).

In contrast to diploids not derived from artificial hybridizations, those derived from artificial hybridizations often formed variable meiotic configurations (Table 3). Notable among crosses producing progeny with variable meiotic configurations was Cross 7 in Table 4 between an 8 II + 1 I seed parent and an 8 II pollen parent. It produced two progeny with variable meiotic configurations. One formed 8 II + 1 I or 7 II + 3 I; the other formed 8 II + 1 I, 8 II + 2 I, 7 II + 3 I, and 7 II + 4 I.

In *E. lanatum* tetraploids, plants with one supernumerary formed 16 II + 1 I; those with two supernumeraries 16 II + 2 I or 17 II, or exclusively 17 II (Table 1).

In *E. confertiflorum* var. *confertiflorum*, diploids formed 8 II + 1 I if one supernumerary was present. One plant with two supernumeraries consistently formed 9 II. Other plants with more than one supernumerary formed 8 II + 2 or 3 I. Tetraploids formed 16 II + 1 I if one supernumerary was present but invariably or frequently formed 17 II if two were present, and 19 II when six were present (Table 2).

The single plant of *E. latilobum* with supernumeraries formed 16 II + 2 I.

Frequency of Supernumerary Chromosomes in *E. lanatum*

The overall frequency of plants and populations with supernumerary chromosomes was 12% (54/459) and 14% (42/293), respectively. Supernumerary chromosomes were not found in the total of 42 plants examined in vars. *croceum*,

hallii, *lanceolatum*, and *obovatum* (Table 1). The frequency of supernumeraries in diploid, tetraploid, hexaploid, and octoploid plants of *E. lanatum* was, respectively, 13% (41/328), 10% (10/103), 0% (0/16), and 18% (2/11). Tetraploids with supernumerary chromosomes appeared limited to vars. *achillaeoides* and *leucophyllum*, and octoploids with supernumerary chromosomes to var. *integrifolium* (Table 1).

The frequency of supernumerary chromosomes varied among populations and varieties, from 34% for individuals and 31% for populations in var. *lanatum* to 4% and 7% in var. *arachnoideum*.

Frequency of Supernumerary Chromosomes in *E. confertiflorum* var. *confertiflorum*

The overall frequency of plants and populations with supernumerary chromosomes was 13% (24/180) and 15% (20/133), respectively. One plant had a fragment chromosome; the rest had normal-sized supernumerary chromosomes. The frequency of supernumerary chromosomes in diploid, tetraploid, hexaploid and octoploid populations was, respectively, 9% (6/69), 22% (13/60), 0% (0/1), and 0% (0/2). One population (143) was mixed, having a diploid with two supernumeraries and two tetraploids with none (Table 2). Only 39% of the diploid populations had supernumeraries, compared to 74% in *E. lanatum*.

Supernumerary Chromosomes in Putative *E. confertiflorum* var. *confertiflorum* × *E. lanatum* derivatives

Eriophyllum latilobum consists of two populations along San Mateo Creek in San Mateo County, California. Individuals formed 16 II except for one that formed 16 II + 2 I. The other putative *E. confertiflorum* var. *confertiflorum* × *E. lanatum* hybrids were tetraploids and hexaploids with one or two supernumerary chromosomes, forming 16 II + 1 I, 17 II, 24 II + 1 I, or 25 II. The frequency of individuals and of populations with supernumerary chromosomes was, respectively, 24% and 50%. The putative hybrid populations were restricted to an approximately 40 km strip in San Mateo and adjacent Santa Clara Counties, California (Table 2).

Transmission of Supernumerary Chromosomes in Artificial Intervarietal and Interspecific Hybridizations in *E. lanatum* and *E. confertiflorum* var. *confertiflorum*

The chromosome number of 13 of the 30 parents in 17 hybridizations (Table 3) was known; the other parents were assumed to form

8 II because representatives of the parental populations formed 8 II. The crosses in Table 3 are divided into four sections and are numbered to facilitate describing the results. Supernumerary chromosomes were transmitted in all crosses.

In Section 1, where the chromosome number of both parents was known, transmission of one supernumerary failed in one of the parents in Cross 1. One supernumerary was transmitted by the seed parent in Cross 2 and by the pollen parent in Cross 3.

In Section 2, where the chromosome number of the seed parent was known, and transmission was through the seed parent, two supernumeraries in Cross 4 and one in Cross 5. In Crosses 6 and 7, transmission probably occurred through the pollen parent, because the seed parent formed 8 II, and supernumeraries had been observed in populations 204 and 205 from which the pollen parents came (Table 1). The origin of supernumeraries in Cross 8 was uncertain. The seed parent formed 8 II, and although supernumeraries were not observed in the pollen parent population (38), the single plant examined in the progeny formed 8 II + 1 I or 7 II + 3 I.

In Section 3, (chromosome number of pollen parent known) the results paralleled those in Section 2. Transmission was through the pollen parent in Crosses 9 and 10, two supernumeraries in Cross 9 and one in Cross 10. In Cross 11, the fragment and supernumerary probably came from the seed parent, S184-1, because supernumeraries occurred in Population 184 (Table 1). The source of the supernumerary in Cross 12 was unknown because supernumeraries were not found in the parental populations.

In Section 4, chromosome numbers were unknown for the parents. Presumably the parents formed 8 II as in their parental populations. The source or sources of the supernumeraries in the progenies was not known (Table 3). All but Cross 15 were either interspecific or intervarietal, and were often between geographically distant populations.

Frequency of Transmission of *E. lanatum* Supernumerary Chromosomes in Artificial Hybridizations

In pre-2000 hybridizations, how frequently supernumeraries were transmitted was unknown because usually only one plant per cross was analyzed (Table 3). Attempts to use reciprocal crosses to estimate transmission frequencies were only partly successful because low percentage germination or failure to flower resulted in only two of five combinations being reciprocal.

The crosses in Table 4 are numbered to facilitate describing the results. The meiotic configuration of the seed parent is known in

Crosses 1–3, and both parents are known in Crosses 4–7. Transmission of one or two supernumerary chromosomes occurred in five of the six progeny in Cross 1, and in 7 of 10 progeny in Cross 2. In Cross 3, the chromosome number of the pollen parent is not known, and the population that furnished it had plants that formed 8 II + 1 I as well as 8 II. If the pollen parent formed 8 II, the supernumerary in the seed parent was transmitted to 9 of the 17 progeny, and multiplied in one of them. A fragment chromosome was also transmitted to three other plants, probably from the pollen parent. Crosses 4 and 5 were reciprocal; the supernumerary chromosome was transmitted when S338-4 was the seed parent but not when it was the pollen parent. However, failure of transmittal through the pollen may be a matter of chance; the progeny consisted of only two plants. Crosses 6 and 7 are reciprocal. Transmission through the pollen parent occurred in 7 of the 18 progeny (39%), compared to 9 of the 14 progeny (64%) for the seed parent.

Pollen fertility figures for progeny with and without supernumeraries did not differ significantly (Table 4).

Nonrandom Geographic Distribution of *E. lanatum* Populations with Supernumerary Chromosomes

Six regions had one to five populations with a high frequency of supernumerary chromosomes. Along the Snake River in Idaho and Oregon, 11 of the 16 plants in five diploid var. *lanatum* populations had one or two supernumeraries. In Trinity County, California, each of three diploid var. *grandiflorum* populations was represented by a plant with two supernumerary chromosomes. In Colusa and Lake Counties, California, two diploid and two tetraploid var. *achillioides* populations were represented by single plants with one supernumerary or one fragment chromosome. In southwestern Oregon (Jackson, Josephine, and Douglas Counties), four of the six plants in tetraploid var. *achillioides* Populations 335 and 62, and var. *leucophyllum* Populations 18 and 337 had one or two supernumerary chromosomes. Also, all four plants in diploid Population 338, an *achillioides-leucophyllum* intermediate, had one or two supernumeraries. Two diploid populations of var. *integrifolium* had high frequencies of plants bearing supernumerary chromosomes. In Adams County, Washington, four of five plants in Population 265 had one to three extra chromosomes. In Elko County, Nevada, each of the single plants in Populations 250 and 251 had four extra chromosomes (Table 1).

TABLE 1. SUPERNUMERARY CHROMOSOMES IN *ERIOPHYLLUM LANATUM* POPULATIONS. Locations within counties are approximate. An asterisk indicates that a univalent was seen to divide at Metaphase I, two asterisks that 9 + 9 disjunctions were seen to occur. The numbers following a taxon name show, respectively, the frequency of individuals and populations with supernumeraries.

Taxa/Location	Population	Meiotic configuration	Number of plants	
			With that configuration	Analyzed
Var. achillioides (8/85 = 9%; 8/61 = 13%)				
CA, Lake Co., Kelseyville	120	8 II + fragment	1	1
Lake Co., Clear Lake	127	8 II + 1 I, 7 II + 1 III	1	1
Siskiyou Co., Dorris	111	8 II + 1 I**	1	2
Colusa Co., Leesville	183	16 II + 1 I	1	1
Lake Co., Clear Lake	132	16 II + 1 I	1	1
Shasta Co., Fall River Mills	153	16 II + 2 I or 17 II	1	1
OR, Jackson Co., Central Point	335	17 II	1	1
Josephine Co., Selma	62	16 II + 1 I	1	1
		Total	8 (89%)	9
Var. arachnoideum (1/24 = 4%; 1/14 = 7%)				
CA, San Mateo Co., Woodside	361	8 II + 1 I	Total	1 (50%)
Var. croceum (0/14; 0/6)				
Var. grandiflorum (5/89 = 6%; 5/57 = 9%)				
CA, Calaveras Co., Murphy's	76	8 II + 1 I	1	2
El Dorado Co., Diamond Springs	179	9 II or 8 II + 2 I	1	1
Trinity Co., Trinity Center	174	9 II or 8 II + 2 I	1	1
Trinity Center	184	9 II	1	1
Trinity Center	221	8 II + 2 I or 9 II	1	1
		Total	5 (83%)	6
Var. hallii (0/3; 0/1)				
Var. integrifolium (16/100 = 16%; 13/60 = 22%)				
CA, Mono Co., Sonora Pass Summit	114	8 II + 1 I	1	2
ID, Blaine Co., Ketchum	257	8 II + 1 I	1	2
Custer Co., Stanley	256	8 II + 1 I	1	2
Owyhee Co., Riddle	252	8 II + 1 I	1	1
NV, Elko Co., Elko	250	10 II	1	1
Elko Co., Mountain City	251	10 II, 9 II + 2 I, 8 II + 1 IV in a few cells	1	1
OR, Deschutes Co., La Pine	108	8 II + 1 I	1	1
Wheeler Co., Antone	271	8 II + 2 I	1	1
WA, Adams Co., Ritzville	265	8 II + 1 I or 9 II	1	5
		8 II + 1 I to 7 II + 3 I	1	
		8 II + 1 I	1	
		9 II + 1 I	1	
WY, Fremont Co., Dubois	56	8 II + 1 I	1	1
Teton Co., Moran	55	8 II + 1 I	1	1
OR, Wasco Co., The Dalles	104	32 II + 1 I	1	1

TABLE 1. CONTINUED.

Taxa/Location	Population	Meiotic configuration	Number of plants	
			With that configuration	Analyzed
WA, Klickitat Co., The Dalles Dam	102	33 II	1	1
		Total	16 (80%)	20
Var. lanatum (11/32 = 34%; 5/16 = 31%)				
ID, Idaho Co., Harpster	30	8 II + 2 I	1	1
Washington Co., Beggs	204	8 II + 1 I	1	3
Washington Co., Brownlee Dam	325	8 II + 2 I	1	4
OR, Baker Co., Oxbow Dam	205	8 II + 2 I to 7 II + 4 I	1	3
Oxbow Dam	324	8 II + 1 I	2	5
		Total	11 (69%)	16
Var. lanceolatum (0/12; 0/8)				
Var. leucophyllum (6/37 = 16%; 6/29 = 21%)				
OR, Douglas Co., Glide	18	16 II + 1 I	1	2
Douglas Co., Azalea	337	16 II + 2 I	1	2
Marion Co., Silverton	94	8 II + 2 I or 9 II	1	1
Multnomah Co., Shepperd's Dell	355	8 II + 2 II*	1	1
WA, Cowlitz Co., Kalama River	172	9 II or 8 II + 2 I	1	1
San Juan Co., Orcas Island	239	8 II + 1 I	1	2
		Total	6 (67%)	9
Var. obovatum (0/13; 0/7)				
INTERGRADES BETWEEN VARIETIES (7/50 = 14%; 4/34 = 12%)				
Var. achillioides-var. arachnoideum (1/12 = 8%; 1/9 = 11%)				
CA, Napa Co., St. Helena	229	17 II	1	1
Var. achillioides-var. grandiflorum (1/17 = 6%; 1/11 = 9%)				
CA, Glenn Co., Stonyford	195	17 II or 16 II + 2 I	1	2
Var. achillioides-var. leucophyllum (4/5 = 80%; 1/2 = 50%)				
OREGON, Douglas Co., Dillard	338	8 II + 1 I	3	4
		8 II + 2 I or 9 II		
Var. arachnoideum-var. grandiflorum (0/2; 0/2)				
Var. grandiflorum-integrifolium (1/3 = 33%; 1/2 = 50%)				
CA, Nevada Co., Emigrant Gap	332	16 II + 1 I	1	3
Var. grandiflorum-var. lanceolatum (0/1; 0/1)				
Var. integrifolium-var. lanatum (0/10; 0/7)				
TOTAL: (54/459 = 12%; 42/293 = 14%)				

TABLE 2. SUPERNUMERARY CHROMOSOMES IN POPULATIONS OF *ERIOPHYLLUM CONFERTIFLORUM* VAR. *CONFERTIFLORUM*, *E. LATILOBUM*, AND PUTATIVE *ERIOPHYLLUM CONFERTIFLORUM* VAR. *CONFERTIFLORUM* × *E. LANATUM* HYBRID DERIVATIVES. Regional and county names are bolded. Locations within counties are approximate. An asterisk indicates that a univalent was seen to divide at Metaphase I. The numbers following the taxon name show, respectively, the frequency of individuals and populations with supernumerary chromosomes. The numbers following a county name show the frequency of populations with supernumeraries. Counties, all in California, are arranged in north to south order, as are populations in them. Percentages are rounded.

Location	Population	Meiotic configuration	Number of plants	
			With that configuration	Analyzed
<i>Eriophyllum confertiflorum</i> var. <i>confertiflorum</i> (24/180 = 13%; 20/133 = 15%)				
South Coast Ranges				
Alameda (1/4), Arroyo Mocho	16	16 II + 1 I	1	1
San Mateo (3/7), Hillsborough	143	8 II + 2 I*	1	2
Montebello Ridge	22	16 II + 1 I	1	2
Portola State Park	142	17 II, 16 II + 2 I	1	2
Santa Clara (3/15), Loma Prieta	10	16 II + 2 I	1	1
Loma Prieta	11	17 II	1	2
Mt. Hamilton	18	16 II + 1 I	1	1
Monterey (4/13), Del Monte	7	16 II + 1 I	1	1
Carmel Valley	25	17 II	2	4
		19 II	1	
Big Sur	107	8 II + 1 I	1	1
Lucia	36	16 II + 1 I	1	2
San Benito (1/10), Pinnacles N. M.	136	17 II	1	1
			Total 14 (70%)	20
Transverse Ranges				
Santa Barbara (2/9), Lompoc	67	16 II + 1 I	1	2
New Cuyama	150	17 II	2	3
			Total 3 (60%)	5
Peninsular Ranges				
San Diego (2/8), Escondido	61	9 II	1	2
Vista	147	8 II + 1 I	1	1
			Total 2 (67%)	3
Sierra Nevada				
Calaveras (1/1), Mokelumne	85	16 II + 1 I	1	1
Mariposa (1/8), El Portal	127	8 II + 1 I	1	1
Tulare (1/5), Mineral King Road	79	8 II + 3 I	1	1
Kern (1/9), Wofford Heights	77	8 II + 1 fragment	1	2
	77	8 II + 2 I	1	
			Total 5 (100%)	5
<i>Eriophyllum latilobum</i> (1/9 = 11%; 1/2 = 50%)				
San Mateo, San Mateo Creek dam	5	16 II + 2 I	1 (33%)	3
Putative natural hybrids, <i>E. lanatum</i> var. <i>arachnoideum</i> × <i>E. confertiflorum</i> var. <i>confertiflorum</i> (6/25 = 24%; 4/8 = 50%)				
San Mateo, Alpine Road	9	16 II + 1-2 I	1	5
Black Mountain	1	24 II + 1 I	2	5
		25 II	1	
Borel Hill	11	17 II	1	3
Santa Clara, Montebello Ridge	6	25 II	1	1
			Total 6 (43%)	14

Nonrandom distribution of *E. confertiflorum* var. *confertiflorum* Tetraploid Populations with Supernumerary Chromosomes

Although the overall ratio of *E. confertiflorum* var. *confertiflorum* diploid to tetraploid populations was 69 to 60, tetraploid populations with supernumeraries outnumbered diploid ones 13 to 6. That ratio rose to 8 to 2 in Monterey, Santa Clara, and San Mateo Counties, California. Only two populations with supernumeraries were found south of Santa Barbara County. They were diploids only 16 km apart, in San Diego County (Table 2).

DISCUSSION

Frequency of Supernumerary Chromosomes Probably Underestimated

I examined only one or two plants in most populations. Larger samples likely would have shown more populations with supernumeraries and different frequencies of supernumeraries in the populations.

Hypotheses for Presence of Supernumerary Chromosomes in *E. lanatum*

Various hypotheses have been proposed to account for supernumerary chromosomes in other species, including adaptive value and meiotic drive that could perpetuate extra chromosomes even if they had deleterious effects. I have no information about *E. lanatum* that would support or discount adaptive value or meiotic drive. Supernumerary chromosomes, however, can be transmitted in *E. lanatum* varieties (Table 3, 4). Also, artificial hybridizations of diploids representing vars. *achillioides*, *grandiflorum*, *integrifolium*, and *lanatum* show that barriers to interbreeding are comparatively low (Mooring 2001, Table 7).

Natural hybridization between chromosomally differentiated populations could lead to gametes with extra chromosomes. The meiotic configurations in the progenies of Crosses 8, 16, and 17 (Table 3) suggest chromosomal restructuring accompanied by the presence of supernumerary chromosomes. Chromosomal restructuring is evident from many other artificial hybridizations between diploids in *E. lanatum* (Mooring 2001).

Except for the Elko County, Nevada, var. *integrifolium* population, all others with a high frequency of supernumerary chromosomes occurred where different varieties meet. The Adams County, Washington, var. *integrifolium* population is adjacent to var. *lanatum* populations. Variety *integrifolium* populations surround the var. *lanatum* populations along the Snake River. Oregon has diploid populations intermediate

between the two varieties (Mooring 2001). Artificial hybridizations between diploids show that barriers to interbreeding are low. Mean percentage pollen fertility of *integrifolium* × *lanatum* progeny was $60 \pm 23\%$ (Mooring 2001, Table 7).

The var. *grandiflorum* populations in Trinity County, California, are in a region where vars. *achillioides*, *grandiflorum*, and *lancoelatum* meet; some populations there are intermediate. Diploid progenies from artificial *achillioides* × *grandiflorum*, *achillioides* × *lancoelatum*, and *grandiflorum* × *lancoelatum* hybridizations have mean pollen fertilities of, respectively, $57 \pm 18\%$, $66 \pm 16\%$, and $68 \pm 16\%$ (Mooring 2001, Table 7).

Similarly, the var. *achillioides* cluster in Lake and Colusa Counties, California, occurs where vars. *achillioides*, *arachnoideum*, and *grandiflorum* merge. Intergrades are numerous (Mooring 2001). Diploid progenies from vars. *achillioides* × *arachnoideum*, *achillioides* × *grandiflorum*, and *arachnoideum* × *grandiflorum* artificial hybridizations had, respectively, pollen fertilities of $74 \pm 8\%$, $57 \pm 18\%$, and $51 \pm 16\%$ (Mooring 2001, Table 7).

Varieties *achillioides* and *leucophyllum* are sympatric in southwestern Oregon. (Variety *achillioides* populations in northern California and southwestern Oregon differ markedly from the southern populations. Variety *ternatum* Greene has been proposed to recognize them.) Differentiating between var. *achillioides* (possibly also var. *ternatum*) and var. *leucophyllum* becomes difficult or impossible, notably in Douglas County, Oregon. Artificial hybridizations between Douglas County Population 338 and two var. *leucophyllum* populations produced diploid progenies whose mean pollen fertility was $78\% \pm 16$ and $81\% \pm 13$ (Mooring, unpublished).

Hypotheses for Nonrandom Distribution of *E. confertiflorum* var. *confertiflorum* Tetraploid Populations with Supernumerary Chromosomes

At least three hypotheses can be made for the nonrandom distribution of *E. confertiflorum* var. *confertiflorum* tetraploid populations with supernumerary chromosomes, especially those in Monterey, Santa Clara, and San Mateo Counties (Table 2): 1) supernumerary chromosomes are adaptive, 2) meiotic drive exists, and 3) local climatic or edaphic conditions affect meiosis and thereby lead to gametes with extra chromosomes. These hypotheses are not mutually exclusive. Two other explanations peculiar to polyploids are: 1) tetraploids tolerate supernumeraries better than diploids, and 2) some plants described as having supernumerary chromosomes may be aneuploids generated by neopolyploids (see Ramsey and Schemske 2002, pp. 601–607).

TABLE 3. ARTIFICIAL INTERVARIETAL AND INTERSPECIFIC HYBRIDIZATIONS IN *ERIOPHYLLUM LANATUM* AND *E. CONFERTIFLORUM* VAR. *CONFERTIFLORUM* THAT PRODUCED PROGENY WITH SUPERNUMERARY CHROMOSOMES. Seed parent is listed first. Only one plant in each progeny was examined meiotically. Each of the 17 crosses is numbered. Bolded chromosome counts are those known for the parent, unbolded those known for the population that furnished it.

Parental taxa and location	Parents	Meiotic configuration
SECTION 1. CHROMOSOME NUMBER OF BOTH PARENTS KNOWN		
<i>Eriophyllum confertiflorum</i> var. <i>confertiflorum</i> × <i>E. lanatum</i> var. <i>lanatum</i> , CALIFORNIA, Mariposa × OREGON, Baker		
1. Eagle Peak × Oxbow Dam	<i>S127-2</i> (8 II + 1 I) × <i>S324-7</i> (8 II + 1 I)	8 II + 1 I
<i>Eriophyllum confertiflorum</i> var. <i>confertiflorum</i> × <i>E. lanatum</i> var. <i>croceum</i> , CALIFORNIA, Mariposa × Fresno		
2. Eagle Peak × Badger	<i>S127-2</i> (8 II + 1 I) × <i>S309-22</i> (8 II)	8 II + 1 I to 6 II + 5 I
<i>Eriophyllum lanatum</i> var. <i>obovatum</i> × var. <i>lanatum</i> , CALIFORNIA, San Bernardino × OREGON, Baker		
3. Running Springs × Oxbow Dam	<i>S289-14</i> (8 II) × <i>S324-3</i> (8 II + 1 I)	8 II + 1 I (I frequently divides at M1)
SECTION 2. CHROMOSOME NUMBER OF SEED PARENT KNOWN		
<i>Eriophyllum lanatum</i> var. <i>integrifolium</i> × var. <i>araclnoideum</i> , WASHINGTON, Adams × CALIFORNIA, Mendocino		
4. Ritzville × Elk	<i>S265-4A</i> (8 II + 2 I) × <i>S212-1</i> (8 II)	9 II, occasional 8 II + 2 I
<i>Eriophyllum confertiflorum</i> var. <i>confertiflorum</i> × <i>E. confertiflorum</i> var. <i>confertiflorum</i> CALIFORNIA, Mariposa × Santa Cruz		
5. Eagle Peak × Bonny Doon	<i>S127-2</i> (8 II + 1 I) × 20 (8 II)	8 II + 1 I
<i>Eriophyllum lanatum</i> var. <i>achillioides</i> × var. <i>lanatum</i> , CALIFORNIA, Yolo, × IDAHO, Washington		
6. Winters × Brownlee Dam	<i>S150-2</i> (8 II) × <i>S204-3</i> (8 II, 8 II + 1 or 2 I)	8 II + 1 I
<i>Eriophyllum lanatum</i> var. <i>integrifolium</i> × var. <i>lanatum</i> , OREGON, Union × OREGON, Baker		
7. Elgin × Oxbow	<i>S267-33</i> (8 II) × <i>S205-34</i> (8 II, 8 II + 1 I)	8 II + 1 I
<i>Eriophyllum lanatum</i> var. <i>lanceolatum</i> × var. <i>achillioides</i> , CALIFORNIA, Humboldt × CALIFORNIA, Santa Clara		
8. Slate Creek × Loma Prieta	280-3 (8 II) × 38-11 (8 II)	8 II + 1 I, 7 II + 3 I
SECTION 3. CHROMOSOME NUMBER OF POLLEN PARENT KNOWN		
<i>Eriophyllum lanatum</i> var. <i>integrifolium</i> × var. <i>lanatum</i> , WYOMING, Yellowstone National Park × IDAHO, Washington		
9. Tower Junction × Brownlee Dam	<i>S58-1</i> (8 II) × <i>S204-1</i> (8 II + 2 I)	8 II + 2 I or 9 II
<i>Eriophyllum lanatum</i> var. <i>araclnoideum</i> × <i>Eriophyllum confertiflorum</i> var. <i>confertiflorum</i> , CALIFORNIA, Mendocino × Los Angeles		
10. Elk × Vincent	<i>S212-1</i> (8 II) × <i>S74-4B</i> (8 II + 1 I)	8 II + 1 I
<i>Eriophyllum lanatum</i> var. <i>grandiflorum</i> × var. <i>grandiflorum</i> , CALIFORNIA, Trinity × CALIFORNIA, El Dorado		
11. Trinity Center × Coloma	<i>S184-1</i> (8 II) × <i>S187-2</i> (8 II)	8 II + 1 I + 1 fragment

TABLE 3. CONTINUED.

Parental taxa and location	Parents	Meiotic configuration
<i>Eriophyllum lanatum</i> var. <i>arachnoideum</i> × var. <i>leucophyllum</i> , CALIFORNIA, San Mateo × OREGON, Multnomah		
12. Woodside × Shepperd's Dell	330-1 (8 II) × S355-4 (8 II)	8 II + 1 I
SECTION 4. CHROMOSOME NUMBER OF NEITHER PARENT KNOWN, THAT OF PARENTAL POPULATION KNOWN		
<i>Eriophyllum lanatum</i> var. <i>achillioides</i> × var. <i>hallii</i> , CALIFORNIA, Santa Barbara × CALIFORNIA, Contra Costa		
13. Mt Diablo × New Cuyama	S306sib (8 II) × S7-3 (8 II)	8 II + 1 I
<i>Eriophyllum lanatum</i> var. <i>arachnoideum</i> × var. <i>obovatum</i> , CALIFORNIA, San Mateo × CALIFORNIA, Kern		
14. Woodside × Greenhorn Summit	330-2 (8 II) × 322-17 (8II)	8 II + 1 fragment
<i>Eriophyllum confertiflorum</i> var. <i>confertiflorum</i> × <i>Eriophyllum confertiflorum</i> var. <i>confertiflorum</i> , CALIFORNIA, San Diego × Santa Cruz		
15. San Diego × Bonny Doon	S120-1 (8 II) × 20 (8 II)	8 II + 1 fragment
<i>Eriophyllum lanatum</i> var. <i>integrifolium</i> × var. <i>integrifolium</i> , WYOMING, Yellowstone National Park × IDAHO, Boise		
16. Tower Junction × Banks	S58-4 (8 II) × S158-8 (8II)	8 II + 1 I, occasional 6 II + 1 IV + 1 I
<i>Eriophyllum lanatum</i> var. <i>grandiflorum</i> × var. <i>leucophyllum</i> , CALIFORNIA, Tehama × WASHINGTON, Island		
17. Payne's Creek × Deception Pass	S199-12 (8 II) × 237-1 (8 II)	6 II + 4 I most frequent, also 8 II, 7 II + 2 I, I sometimes divides, 7 II + 3 I, 6 II + 5 I, 5 II + 1 III + 1 I

Supernumerary Chromosomes and Dysploidy

In *Eriophyllum*, as presently constituted, base chromosome numbers are $n = 4, 5$, and 7 for the annual species and $n = 8$ for the perennial species. Two annual species have extra chromosomes. Counts for *E. wallacei* are $5 \text{ II} + 0-1 \text{ I}$ (Taylor 1967; Strother 1972, 1976; Johnson 1978), and $5 \text{ II} + 0-3 \text{ B}$ chromosomes (Johnson 1978). Counts for *E. pringlei* are $7 \text{ II} + 0-1$ centric fragment (Strother 1972, 1976), 8 II (Keil and Pinkava 1976), $7 \text{ II} + 0-1 \text{ I}$ and $7 \text{ II} + 0-3 \text{ B}$ chromosomes (Johnson 1978). Supernumerary chromosomes are also present in the perennial eriophyllums. *Eriophyllum lanatum* has one to four supernumerary chromosomes; *E. confertiflorum* var. *confertiflorum* has one, two, or six supernumerary chromosomes.

Grant (1981, pp. 358–360) referred to a base haploid chromosome number series of $8-7-()-4-3$ in *Eriophyllum* and *Pseudobahia* as an example of “descending aneuploidy” derived by unequal reciprocal translocations. (The symbol () indicates missing intermediate numbers.) However, supernumerary chromosomes may also have been

involved in the formation of the dysploid series. Supernumerary chromosomes might have become members of the A complement, especially if they are trisomics. Alternatively, extra chromosomes might be obtained by interspecific hybridizations. Lewis (1953) suggested that ascending dysploidy ($x = 7, 8$, and 9) in *Clarkia* may have involved the acquisition of supernumerary chromosomes or the occurrence of interspecific hybridizations. Lewis and Roberts (1956) described the origin of *Clarkia lingulata* ($n = 9$) from *C. biloba* ($n = 8$) by the addition of a tertiary trisomic.

It is interesting that base haploid chromosome numbers in the closely related genera *Eriophyllum*, *Syntrichopappus*, and *Pseudobahia* (Baldwin and Wessa 2000) form the dysploid series $8-7-6-5-4-3$. Perhaps significantly, *P. heermannii* (Durand) Rydb. has three base haploid chromosome numbers and chromosomes in excess of the basic complement, $2n = 6 + 0-2 \text{ I}$, $2n = 8 + 0-1 \text{ I}$ or $0-1 \text{ B}$, and $2n = 10 + 0-1 \text{ I}$ (Johnson 2006). For the past three years, I have been maintained an artificial hybridization program in *Pseudobahia heermanni* to analyze meiosis, detect barriers to

TABLE 4. FREQUENCY OF SUPERNUMERARY CHROMOSOMES IN PROGENY FROM ARTIFICIAL HYBRIDIZATIONS IN *ERIOPHYLLUM LANATUM*. Seed parent is listed first. Bolded chromosome counts are those known for the parent, unbolded those known for the population that furnished the parent. State and county names are bolded. Locations within counties are approximate. The crosses are numbered to facilitate explanations. NCD = no chromosome number data; meiosis was not examined in that parent, and 8 II and 8 II + 1 I are known in that population. Figures in parentheses in progeny columns are pollen fertility percentages ± 1 SD.

Taxa, parental location, cross	$2n$ number of chromosomes (and % pollen fertility of progeny)				
	16	17	17 + fragment	18	N
Var. <i>achillioides-leucophyllum intermedia</i> \times var. <i>leucophyllum</i> , OREGON, Douglas, Dillard \times Wasco, Rowena					
1. <i>S338-6</i> (8 II + 2 I) \times <i>S342-6</i> (8 II)	1 (89)	3 (66 \pm 20)	0	2 (73 \pm 6)	6
Var. <i>leucophyllum</i> \times var. <i>obovatum</i> , OREGON, Multnomah, Shepperd's Dell \times CALIFORNIA, Kern, Greenhorn Summit					
2. <i>S335-6</i> (8 II + 2 I) \times <i>S22A-10</i> (8 II)	3 (29 \pm 5)	3 (27 \pm 2)	0	4 (27 \pm 9)	10
Var. <i>achillioides-leucophyllum intermedia</i> \times var. <i>achillioides</i> , OREGON, Douglas, Dillard \times CALIFORNIA, Napa, Calistoga					
3. <i>S338-4</i> (8 II + 1 I) \times <i>118-2</i> (NCD)	4 (80 \pm 11)	9 (71 \pm 10)	3 (66 \pm 10)	1 (67)	17
Var. <i>achillioides-leucophyllum intermedia</i> \times var. <i>achillioides</i> , OREGON, Douglas, Dillard \times OREGON, Josephine, Galice					
4. <i>S338-4</i> (8 II + 1 I) \times <i>S350-13</i> (8 II)	1 (51)	1 (52)	0	0	2
5. R	2 (75 \pm 26)	0	0	0	2
Var. <i>achillioides</i> \times var. <i>achillioides</i> , CALIFORNIA, Napa, Calistoga					
6. <i>118-4</i> (8 II) \times <i>118-5</i> (8 II + 1 I)	11 (85 \pm 17)	7 (87 \pm 11)	0	0	18
7. R	5 (74 \pm 24)	9 (75 \pm 37)	0	0	14

interbreeding, and see if the extra chromosomes can be transmitted. The extra chromosomes can be transmitted (Mooring unpublished).

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